

# THE INFLUENCE OF HOST FRUIT MORPHOLOGY ON PARASITIZATION RATES IN THE CARIBBEAN FRUIT FLY, *ANASTREPHA SUSPENS*A

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Among the host fruits of the Caribbean fruit fly there are a variety of sizes and shapes. These morphological differences may influence the vulnerability of the larvae to parasites. In the laboratory, Caribbean fruit fly larvae placed in the smaller of 2 different sizes of artificial 'fruit' (cloth spheres filled with a diet material) were parasitized at a higher rate by the braconid, *Diachasmimorpha longicaudata* (Ashmead) when spheres were presented separately. However, when parasites were simultaneously presented with 6 different sizes of 'fruit' there was no significant relationship between size and parasitization rate. This may be due to the parasites preference to search for larvae in larger 'fruit'. In field collections of different species of host fruit, a significant inverse correlation exists between fruit radius and rate of parasitization. However, host fruit size accounts for only about 5 % of the variance in yearly parasitization rates.

KEY-WORDS: *Anastrepha*, *Diachasmimorpha*, host vulnerability, density-dependent mortality, inundative release, *Biosteres*.

Fruit is both a feast and a fortress to maggots of tephritid flies. Morphological characteristics of a host fruit can influence maggot vulnerability to natural enemies (see **Price et al.**, 1980). For example, apple maggots *Rhagoletis pomonella* (Walsh) in apples are less often attacked by the braconid *Biosteres* (= *Opius*) *melleus* (Gahan) than when they occur in native fruit such as hawthorne (*Crataegus* spp.). It is believed that the smaller size of the hawthorne puts a greater proportion of larvae within range of parasite ovipositors (**Porter**, 1928). Similar effects are also known from other cloistered insects that occur inside different sizes of leaf buds and under different thicknesses of bark (e.g., **Graham & Baumhofer**, 1927).

The Caribbean fruit fly, *Anastrepha suspensa* (Loew), is a subtropical pest of at least 90 fruit species in 23 families (**Swanson & Baranowski**, 1972). These hosts have a considerable range of sizes and seed morphologies that might influence the depth at which larvae can feed, and hence affect their exposure to parasitoids.

The larval-pupal opiine braconid, *Diachasmimorpha* (= *Biosteres*) *longicaudata* (Ashmead) is the parasite most likely to attack Caribbean fruit fly larvae in South Florida. Originally from the Asian tropics, *D. longicaudata* was introduced into Florida via Hawaii in 1969 (**Baranowski**, 1974). It quickly became established and was estimated to have reduced the caribfly population by as much as 40 % (**Baranowski**, 1987).

This report describes the relationship between the size of artificial 'fruit' (diet material held in spherical shapes by fine cloth) and the rate of parasitization by *D. longicaudata* of the Caribbean fruit fly larvae they contain. Correlations in the field between parasitization rate and host fruit size and the distribution of edible tissue about the seed(s) are examined. The importance of host fruit size on design of inundative releases of the parasite is discussed.

## MATERIALS AND METHODS

Two factors associated with fruit size are likely to be important in determining parasitization rates. These factors are, 1) depth beneath the surface at which larvae feed, and 2) the preference of adult parasites to forage on certain sizes of fruit. In order to determine the probability of a caribfly larva being within a parasite's reach, 2 different sizes of artificial 'fruit' were constructed. These consisted of either 108 g or 9 g of a larval fruit fly diet (see Sivinski & Calkins, 1990) shaped by fine cloth into spheres of 22.5 cm and 9.2 cm circumferences, respectively. The larger sphere contained 36 six-day-old Caribbean fruit fly larvae. Three, six-day-old larvae were placed in the smaller sphere. Larval densities were similar to those found in a year-long field survey (see following section on parasitization rates in field collected fruit). The artificial fruit spheres were then suspended from the ceilings of 56 × 56 × 56 cm organza cloth cages. A single large sphere in one cage was exposed for 24 h to 36 three- to seven-day-old female *D. longicaudata*. Parasites were obtained from a colony maintained for over 2 years at the USDA/ARS Insect Attractants, Behavior, and Basic Biology Laboratory at Gainesville, Florida. Twelve of the small spheres in the other cage were likewise suspended and similarly exposed to parasitization. A fresh set of spheres was created after 24 h and exposed to the alternate parasites; i.e., the new single large sphere was introduced into the cage that immediately before had held 12 small spheres and vice versa. Parasites were given water and honey during their 48 h exposure to artificial fruit. In the 6 replicates performed, 432 larvae in 12 large spheres and 432 larvae in 144 small spheres were exposed to parasitization. Lights were on a 12L : 12D schedule. Temperature was maintained at 25 °C (± 1°) and the relative humidity varied between 60-80 %. Mean parasitization rates were compared by the Wilcoxon paired test (Zar, 1974).

In the 1<sup>st</sup> experiment, parasites were not given a choice as to which size sphere they could search for larvae upon. If parasites prefer to search for larvae in certain size fruits, then the risks to fly larvae in those fruits may be greater. Various sizes of artificial 'fruit' spheres were constructed in order to determine the vulnerability to parasitization of maggots dwelling in different size hosts when parasites are free to forage. These again consisted of larval diet held into a spherical shape by a covering of organza cloth, and containing different numbers of 6 day old Caribbean fruit fly larvae. The characteristics of different sphere sizes were as follows: 1) 6.2 cm circumference, 3 g weight, contained 1 larva; 2) 8.2 cm circumference, 6 g weight, contained 2 larvae; 3) 10.7 cm circumference, 12 g weight, contained 4 larvae; 4) 13.8 cm circumference, 25 g weight, contained 9 larvae; 5) 17.2 cm circumference, 20 g weight, contained 18 larvae; and 6) 22.5 cm circumference, 100 g weight, contained 35 larvae. These sphere sizes reflect the range of Caribbean fruit host sizes and the larval densities are similar to mean numbers of larvae/g of host fruit found in a year-long field survey (see the subsequent portion on parasitization rates in the field). All spheres were simultaneously hung from the ceiling of a 56 × 56 × 56 cm organza cloth cage. Initial placement was random and spheres were then rotated to the adjacent position after each replicate. Each cage contained 69 female *Diachasmimorpha longicaudata*, 3-7 days old. Exposure of maggots to wasps began at 15.00 h and continued for 24 h.

Every 30 min between 08.00 and 16.30 h, the number of parasites on the surface of a sphere was recorded. Exposed maggots were removed from the diet after 24 h and handled in the previously described manner. There were 12 replicates. Statistical analysis was by regression and ANOVA/Duncan's separation of means test (SAS Institute, 1982).

#### PARASITIZATION RATES IN FIELD COLLECTED FRUIT

Fruits were collected monthly in Dade County, Florida for one year (Oct. 1987-Sept. 1988). Collection sites were: 1) USDA-ARS Subtropical Horticultural Research Unit (Surinam cherry, *Eugenia uniflora* L.; loquat, *Eriobotrya japonica* (Thunb.) Lindl.; guava *Psidium guajava* L.), 2) IFAS Tropical Agricultural Research and Education Center (Surinam cherry, loquat, guava, Cattley guava, *Psidium cattleianum* Sabine; Pitomba, *Eugenia luschnathiana* Klotzch), 3) Redlands Fruit and Spice Park (Surinam cherry, guava, Cattley guava), and 4) Crandon Park, Key Biscayne (tropical almond; *Terminalia catappa* L.). Fruits were either picked ripe from the plant, or taken from the ground if they were firm and apparently freshly fallen. The location of each fruit (whether on or off the tree) was recorded as was the equatorial diameter of the fruit and its weight. A separate subsample of each species of fruit ( $n = 10-20$ ) was weighed. The seed(s) were then dissected out and weighed separately. These data were used to calculate the relationship between fruit weight and seed size, allowing for estimation of seed size in non-dissected fruit used for sampling insects. Fruits were individually placed according to size in 175, 300, or 500 ml plastic cups partially filled with damp vermiculite. Cups and contained fruit were held at 25 °C and 80 % RH. Water was added to cups as needed to maintain a moist environment. Seven days after placing fruit in cups, the vermiculite was sifted for *A. suspensa* pupae and fruit was examined for flies which pupated within the fruit. Pupae were counted, then returned to the damp vermiculite, held at 25 °C and 80 % RH, and checked periodically for adult fly and/or parasite eclosion (about 14 days after sifting). Adult insects were sexed and counted daily. Emerged parasitoids, identified by the author, were retained in the author's collection for further examination. In addition to *D. longicaudata*, the braconids *Doryctobracon areolatus* (Szepligeti) and *Bracnastrepha anastrephae* (Viereck) were also noted. These species, which together comprised less than 5 % of the parasite fauna, were excluded from analyses. Samples of fruit sizes varied with fruit availability and ranged from 1 to > 100. The fruits collected during the 12 month study totalled 1,306.

The parasitization rate in a single fruit was the total number of *D. longicaudata* it produced divided by the sum of flies and parasites it yielded. The depth of fruit pulp (adjusted radius) was estimated by multiplying the proportion (by weight) of the fruit not occupied by seed with the fruit radius. This assumes that fruit is spherical, that seeds and fruit have the same density and that seeds are in the center of fruit, i.e., equidistant from all points on the surface. Since a volume relationship (proportion by weight) is used to derive a linear value (radius) the calculation must take into effect the fact that volume of a seed increases disproportionately with the surface of the seed, hence:

Fruit depth (i.e. adjusted radius)

= radius of the fruit — radius of the seed

or

= radius of the fruit —  $\frac{3\sqrt{(\text{volume of the seed})}}{4}\pi$

if the volume of the fruit occupied by seed is represented by the proportion of the fruit occupied by seed

then

= radius of the fruit —  $(1 - 3\sqrt{\text{proportion of the fruit occupied by seed}})$

Another measurement of fruit depth that did not require as many assumptions but is not as easily visualized (grams of fruit pulp per cm<sup>2</sup> of fruit surface) is also used throughout and does not materially change the results. Statistical analysis included correlation, t-test, paired t-test, and ANOVA/Duncan's separation of means test (SAS Institute, 1982).

## RESULTS AND DISCUSSION

When parasites were caged with one size of artificial 'fruit' sphere and unable to choose which size to search for larvae upon, parasitization rates were higher in the smaller sphere ( $p < 0.05$ , table 1). When different sizes of artificial spheres were presented simultaneously, there was no linear relationship between size and parasitization rate ( $p = 0.59$ ; see fig. 1). It should be noted that the recovery of adults from the 3 smaller sphere sizes averaged only 13 % compared to 28 % for the larger sizes. This resulted in adults being recovered from only 2 replicates of the 3 g spheres, 2 replicates of the 6 g spheres and 4 replicates of the 12 g spheres. When the 25, 50, and 100 g spheres were considered from which respectively 9, 11 and 11 replicates yielded adults, there was again no relationship between sphere size and parasitization rate ( $p = 0.58$ ). However, parasites were more likely to visit larger spheres ( $p = 0.0001$ , fig. 1). Thus, the number of parasite visits/larva is statistically similar across sphere sizes (fig. 2,  $p = 0.06$ ). An exception is the 10.7 cm diameter sphere which attracted significantly more parasites/larva than the other sizes and which had a relatively higher (though not significantly higher) parasitization rate as well ( $p > 0.05$ , fig. 2, table 2). It would appear that while larvae in smaller fruit are more vulnerable to parasitization, the preference of *D. longicaudata* for large fruit containing on average more hosts might mitigate that vulnerability.

Fruit collections were made to determine the importance of host-fruit size on larval mortality in the field. The insects from fallen fruit were compared to ripe-hanging fruit to determine if they represented a homogeneous sample of flies and parasites. Fresh-fallen fruit might have been slightly older, and thus contain greater numbers of mature maggots which had been exposed longer to parasites. Mean numbers of *A. suspensu* pupae from

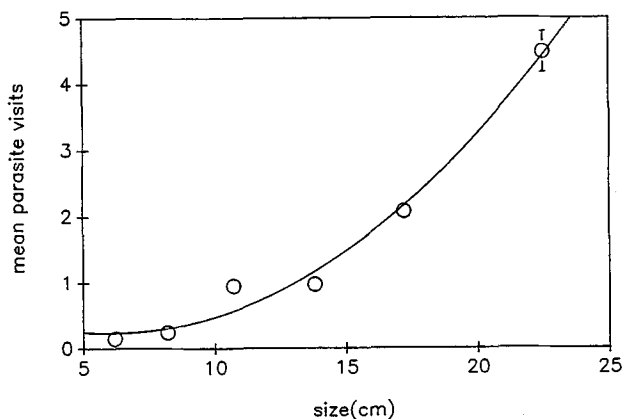


Fig. 1. The mean number of parasites observed on the surface of an artificial 'fruit' sphere during any one observation period in relation to the size of the 'sphere'. Cross bars represent standard errors ( $r^2 = 0.29$ ).

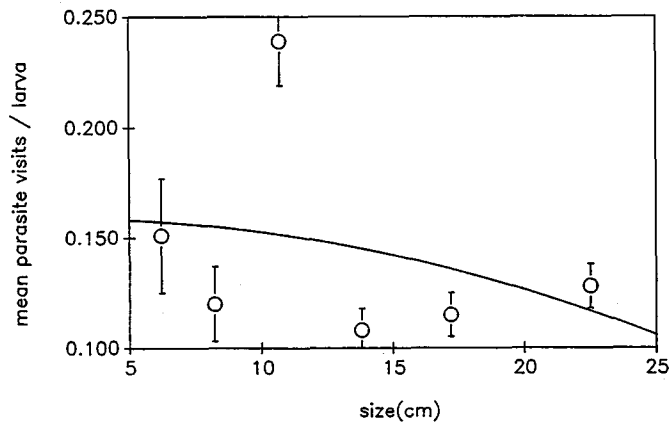


Fig. 2. The Y axis represents the mean number of parasites observed on the surface of an artificial 'fruit' sphere divided by the number of Caribbean fruit fly larvae the 'sphere' contains. The X axis represents the size of the fruit. Cross bars represent standard errors ( $r^2 = 0.003$ ).

TABLE I

*The mean parasitization rate and standard error of larvae occupying either 12 large (22.5 cm cir.) or 144 small (9.2 cm cir.) artificial hosts*

	Large ball (108 g)	Small balls (9 g)
Mean percent parasitization	33	54
Standard error	15	17
Number of adult insects eclosing	50	53

TABLE 2

*Mean parasitization rates and standard errors of the means for different size artificial host fruit*

Sphere size (cm)	Mean parasitization rate (SE)
6.2	.50 (.50)
8.2	.50 (.50)
10.7	.75 (.25)
13.8	.60 (.13)
17.2	.75 (.08)
22.5	.66 (.10)

fallen and on-tree fruit and the mean parasitization rates of these flies were compared in a pair-wise fashion (e.g., on and off guava trees from site 1, collected in October, or on and off the Surinam cherry from site 2, collected in June, etc.).

Hanging and freshly fallen fruit did not differ in numbers of larvae contained ( $n = 31$  samples,  $\bar{x}$  difference [where difference = hanging-fallen fruit] =  $-0.83$ , std err =  $0.57$ ,  $p = 0.15$ ). Differences in mean parasitization rates were also not significant ( $n = 24$  samples,  $\bar{x}$  difference [where difference = hanging-fallen fruit] =  $-0.05$ , std err =  $0.03$ ,  $p = 0.06$ ). Data from hanging and fallen fruit were thus combined to maximize sample sizes.

The Caribbean fruit fly is not uniformly distributed in the fruit species (table 3). Among the 6 fruit species sampled a strong correlation exists between mean fruit weight and the mean number of insects contained ( $r = 0.97$ ,  $p < 0.002$ ). Actual fly density (insects/gram weight) is greatest in the 2 *Eugenia* spp., Surinam cherry and pitomba (table 3). Differences in density may be due to differences in the quality of the fruit (i.e., its ability to attract oviposition and sustain larvae) or may reflect differences in the adult fly population during the seasonally distinct fruiting periods of most of these species (e.g., loquat, with the lowest mean density, fruits in the late winter and early spring when the adult fly population is believed to be low; perhaps for reasons other than the quality of available fruit).

Flies infesting different fruit species bear significantly different rates of parasitization (table 3) and differences in the fruit sizes and morphologies could affect the access parasites have to fly larvae (table 3). However, simple weight and diameter might be misleading in terms of exposing maggots to parasitization. For example, tropical almond has a relatively thin layer of fly-inhabited tissue stretched over a large seed-containing husk. While its diameter is greater than that of pitomba, Surinam cherry, and Cattley guava, its pulp (adjusted radius) is shallower (table 3). On the other hand, adjusted radius will underestimate the depth under the fruit surface at which maggots can live in guavas since seeds occur in a loose central aggregate and flies can feed among them. Pitomba, Surinam cherry and loquat all have tight central seed masses. Note that the mean ovipositor sheath length of *D. longicaudata* is only 4.4 mm (SE = 0.5 mm,  $n = 44$ ; personal observation) and that this is less than the adjusted radii of all the host fruits. A fly larva might be beyond reach at some point in any of these fruit species. Alternatively, larvae leaving their host to pupate in the soil would be exposed as they moved toward the surface of even the largest fruit. Larvae just prior to pupation are less likely to be successfully parasitized by *D. longicaudata* than slightly younger larvae (Lawrence *et al.*, 1976). Perhaps this relative immunity is an adaptation of the larva to protect it during a particularly dangerous time in its development.

Among species, mean fruit size is not significantly correlated to parasitization rate ( $r = -0.61$ ,  $p = 0.20$ ). However, the smallest fruit are more heavily parasitized and the largest fruits are among the least parasitized (see table 3). When all data were pooled, there was a significant inverse correlation between parasitization rate and the adjusted radius ( $r = -0.21$ ,  $n = 786$ ,  $p < 0.0001$ ; grams of fruit pulp/cm<sup>2</sup> of fruit surface correlated to parasitization rate,  $r = 0.20$ ,  $p < 0.0001$ ). Data gathered over the entire year are not strictly comparable. Variables other than size that might affect parasitization rates and be different at various sample sites and times are not taken into account (e.g., adult parasite density, foraging ability of the parasite in a particular host, and weather). Peak host fruiting seasons do not overlap extensively, but in five instances where samples of two species were obtained from the same site and at the same time, the smaller fruit did not have significantly higher parasitization rates. Correlations between parasitization rate and adjusted radius *within* particular samples are rare. In 25 subsamples of a particular fruit species from one place and time, 2 significant correlations were discovered and both of these were, contrary to expectation, positive (loquat, adjusted radius correlated to parasitization rate,  $r = 0.30$ ,  $n = 49$ ,  $p < 0.03$ ; grams of fruit pulp/cm<sup>2</sup> of fruit surface correlated to parasitization rate  $r = 0.36$ ,  $p < 0.01$ ; guava, adjusted radius correlated to

TABLE 3

*The means (standard error) of various fruit and insect fauna parameters. Means in columns sharing a letter are not significantly different*

	N	Weight (-seed) (g)	Adjusted radius (cm)	Number of insects	g of fruit pulp/cm <sup>2</sup> of fruit surface	Insect density (insects/g)	Parasiti- zation rate
Pitomba	102	2.4 (0.1 )c	0.74 (0.01)e	1.0 (0.10)b	0.22 (.00)d	0.44 (0.05)b	0.45 (0.06)a
Surinam Cherry	371	3.0 (0.07)	0.82 (0.02)d	1.7 (0.09)b	0.23 (.01)d	0.60 (0.03)a	0.43 (0.03)ab
Cattley Guava	90	5.5 (0.3 )bc	0.90 (0.02)c	1.1 (0.16)b	0.29 (.01)c	0.21 (0.04)de	0.08 (0.04)d
Tropical Almond	90	6.5 (0.12)bc	0.61 (0.0 )f	2.8 (0.42)b	0.21 (.00)d	0.41 (0.06)bc	0.33 (0.05)bc
Loquat	318	9.7 (0.3 )b	1.1 (0.01)b	1.0 (0.09)b	0.46 (.01)b	0.11 (0.01)e	0.26 (0.03)c
Guava	291	52.6 (2.4 )a	1.9 (0.03)a	14.0 (0.94)a	0.63 (.01)a	0.32 (0.02)cd	0.13 (0.01)d

parasitization rate,  $r = 0.55$ ,  $n = 14$ ,  $p < 0.04$ , grams of fruit pulp/cm<sup>2</sup> of fruit surface correlated to parasitization rate  $r = 0.66$ ,  $p < 0.02$ ).

Less than 5 % of the variance in parasitization rates over a period of a year is accounted for by the size of host-fruit. Other factors, perhaps environmental parameters, or lack of synchrony between host and parasite populations, probably play a greater role in the determination of parasitization rate (see discussion of oscillation of specialist parasite numbers in Hassell, 1986). The female preference for larger fruit displayed in the laboratory would minimize differences in parasitization rates within a sample of fruit from a particular time and place.

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#### RÉSUMÉ

Influence de la morphologie du fruit hôte sur les taux de parasitisme  
chez la mouche des fruits des Caraïbes  
*Anastrepha suspensa*

Il existe une grande variété de tailles et de formes parmi les fruits-hôtes de la Mouche des fruits des Caraïbes. Ces différences morphologiques peuvent influencer la vulnérabilité des larves vis-à-vis des parasites. Au laboratoire, des larves de la mouche des fruits des Caraïbes placées dans le plus petit des deux « fruits » artificiels de taille différente (sphères de tissu remplies avec un milieu alimentaire) étaient parasitées à un niveau plus élevé par le braconide *Diachasmimorpha longicaudata* (Ashmead)

quand les sphères étaient présentées séparément. Cependant, quand les parasites furent présentés simultanément avec six tailles différentes de « fruit », il n'y avait pas de relation significative entre la taille et le taux de parasitisme. Ceci peut être dû aux préférences des parasites à rechercher les larves dans les fruits plus gros. Dans les récoltes à l'extérieur de différentes espèces de fruit hôte, il existe une corrélation inverse significative entre le rayon du fruit et le taux de parasitisme. Cependant la taille du fruit hôte ne compte seulement que pour environ 5 % de la variance dans les taux annuels de parasitisme.

**MOTS CLÉS :** *Anastrepha*, *Diachasmimorpha*, vulnérabilité de l'hôte, mortalité, facteur densité, lâcher inondatif.

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